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# USE OF MULTI-LAYER CAMERA TRAPPING TO INVENTORY MAMMALS IN RAINFORESTS IN SOUTHEAST CAMEROON

HONGO Shun
*The Centre for African Area Studies, Kyoto University, Japan*
*Institute of Agricultural Research for Development, Cameroon*

DZEFACK Zeun's C.B.
*Projet Coméca, Cameroon*

VERNYUY Latar N.
*Faculty of Science, University of Yaoundé I, Cameroon*

MINAMI Sosuke
*Graduate School of Asian and African Area Studies, Kyoto University, Japan*

NAKASHIMA Yoshihiro
*College of Bioresource Sciences, Nihon University, Japan*

DJIÉTO-LORDON Champlain
*Faculty of Science, University of Yaoundé I, Cameroon*

YASUOKA Hirokazu
*The Centre for African Area Studies, Kyoto University, Japan*

ABSTRACT Species richness is a basic metric for ecological study and wildlife management. However, complete mammal species lists are often unavailable for African rainforest areas. We conducted a multi-layer camera trap survey wherein arboreal and terrestrial cameras were concurrently deployed to inventory mammals in the rainforests in and around Boumba-Bek and Nki National Parks in southeast Cameroon. We deployed 88 terrestrial and 150 arboreal cameras with the aid of Baka assistants. From a total of 2,901 terrestrial and 5,404 arboreal camera-days, we obtained 7,359 terrestrial and 4,433 arboreal mammal video records and recorded 40 species and one genus-level taxon (*Galagoides* spp.). Among these, 4 were observations of nocturnal arboreal mammals that had not previously been documented in the study area. Arboreal cameras captured all but 1 of the arboreal species previously recorded in the study area. In contrast, terrestrial cameras failed to capture 4 previously observed species. Our survey captured more primate and carnivore species than any previous study in the area, demonstrating the efficacy of this approach for inventorying mammals in African rainforests.

Key Words: Arboreal camera trap; Boumba-Bek National Park; Mammal community; Nki National Park; Species richness.

## INTRODUCTION

Obtaining species richness data is fundamental to ecological research (Waide et al., 1999; Hurlbert & Jetz, 2007) as well as conservation and management (Conroy & Noon, 1996; Zipkin et al., 2009). African mammal communities are frequently in the wildlife management spotlight due to their importance to tourism (Okello et al., 2008), conservation planning (Roberge & Angelstam, 2004; Branton & Richardson, 2011), and local food security (Asibey, 1974; Fa et al., 2003). However, accurate and complete mammal species lists are not always available for African tropical rainforests, even within protected areas, because of poor visibility in these dense forests and the substantial field effort required to compile such lists. Mammal inventories in African rainforests are typically conducted using transect and/or reconnaissance (recce) methods to obtain species occurrence data from direct observations, along with indirect evidence such as vocalizations, scat, and tracks (White & Edwards, 2000). However, direct observations of unhabituated mammals are typically only seconds long, and identifying species from indirect evidence is difficult (Furuichi et al., 1997; van Vliet et al., 2008); both of these factors inhibit researchers from compiling accurate lists.

Camera traps, motion-triggered automatic cameras carrying a passive infrared sensor (Apps & McNutt, 2018), have gained popularity in field ecology over the last 30 years, and camera trapping has rapidly become one of the principle methods used in mammal ecology (Rovero et al., 2013; Burton et al., 2015; Agha et al., 2018; Hongo, 2018). Although this technique is frequently used to estimate the abundance and density of specific species (Karanth, 1995; O'Brien et al., 2003; Karanth et al., 2004; Rowcliffe et al., 2008; Rovero & Marshall, 2009; Royle et al., 2009; Nakashima et al., 2018), camera traps are also widely used to inventory mammal communities in various environments around the world (Rovero & De Luca, 2007; Norris et al., 2012; Naing et al., 2015; de Oliveira et al., 2016), including central African tropical rainforests (Vanthomme et al., 2013; Nakashima, 2015; Bruce et al., 2018; Hedwig et al., 2018; Orban & Kabafouako, 2018). Most previous studies in forest habitats have installed cameras 0.3–1.5 m from the ground and focused almost exclusively on terrestrial species. Consequently, the mammal species lists resulting from these studies are often incomplete, as they fail to capture many arboreal species. Arboreal mammals are often nocturnal and elusive, making them difficult to detect using conventional transect or recce methods.

Field ecologists have recently begun to deploy cameras higher in trees to record tree-dwelling mammals. Arboreal camera trapping has been used to monitor animals traveling in the high canopy (Gregory et al., 2014) and to observe specific mammal taxa (Di Cerbo & Biancardi, 2012; Olson et al., 2012; Suzuki & Ando, 2019). Arboreal camera traps were successfully used to estimate mammal species richness in rainforest canopies in South America (Oliveira-Santos et al., 2008; Whitworth et al., 2016; Bowler et al., 2017), validating the efficacy of this approach. To our knowledge, no research has utilized arboreal camera trapping in African rainforests. Furthermore, researchers have yet to investigate the concurrent use of camera traps targeting both terrestrial and arboreal mammals.

Southeast Cameroon is located in the northwest portion of the Congo basin tropical rainforest (Corlett & Primack, 2011). This area represents the Cameroonian segment of the Tri-National Dja-Odzala-Minkébé (TRIDOM) landscape; it contains two national parks (Boumba-Bek and Nki) and harbors a wide variety of mammals, including several species of forest duikers (Kamgaing et al., 2018). Therefore, wildlife management is of particular interest in this region (De Wachter et al., 2009). Researchers (Bobo et al., 2014) and a collaborative team comprising government and World Wildlife Fund (WWF) staff (Nzooh Dongmo et al., 2016) previously conducted field inventories in this area to assess mammal distribution and abundance using transect and recce methods. Despite substantial effort, their resulting mammal species list appeared to be incomplete due to several factors. First, many species were observed indirectly. Second, the lists appear to lack some species and include species whose presence in the area is doubtful, particularly with regard to arboreal primates. Finally, forest duikers were categorized as "red duikers" or "small-, medium-, or large-sized duikers," although these classifications include several species. No camera trap inventory has been published for either of the two national parks.

We conducted a camera trap survey with the goal of compiling a complete mammal species list for a rainforest area in southeast Cameroon. We deployed concurrent camera traps in terrestrial and arboreal habitats with the assistance of Baka hunter-gatherers. We then compiled a species list of terrestrial and arboreal mammals in our study area by combining the information gained from camera trapping with previously recorded direct observational data. We also compared our results with previous studies in the study area to examine the efficiency of camera trapping for this region.

## METHODS

### I. Study Area

The study area was located in the northern portions of Boumba-Bek and Nki National Parks and adjacent community hunting zones (CHZs) 13 and 14 (Fig. 1). Local Baka and Konabembe (Bantu) people live and engage in agriculture, hunting, and plant collection within these CHZs. The study area consists primarily of evergreen and semi-deciduous forests (Letouzey, 1985), and an unpaved public road passes through the area from northeast to southwest. Our research station, Gribé IRAD Antenna, was located at N 3°00′ and E 14°49′. The annual rainfall in the study area is approximately 1,500 mm, and the mean annual temperature is 24.0°C (Nzooh Dongmo et al., 2016). Typically, the dry season occurs from December to February, and the rainy season from March to November, but there is little rain during July and August in some years.

### II. Camera Trapping

We conducted camera trap surveys from September 26, 2018, to February 2, 2019, using Browning® Strike Force HD Pro (model BTC-5HDP; Prometheus Group, Birmingham, AL, USA) cameras. Cameras were configured to record a video image in response to the passage of animals. The minimum interval between videos was set to 1 s. The time length per video was set to 10 s and 20 s for arboreal and terrestrial cameras, respectively.

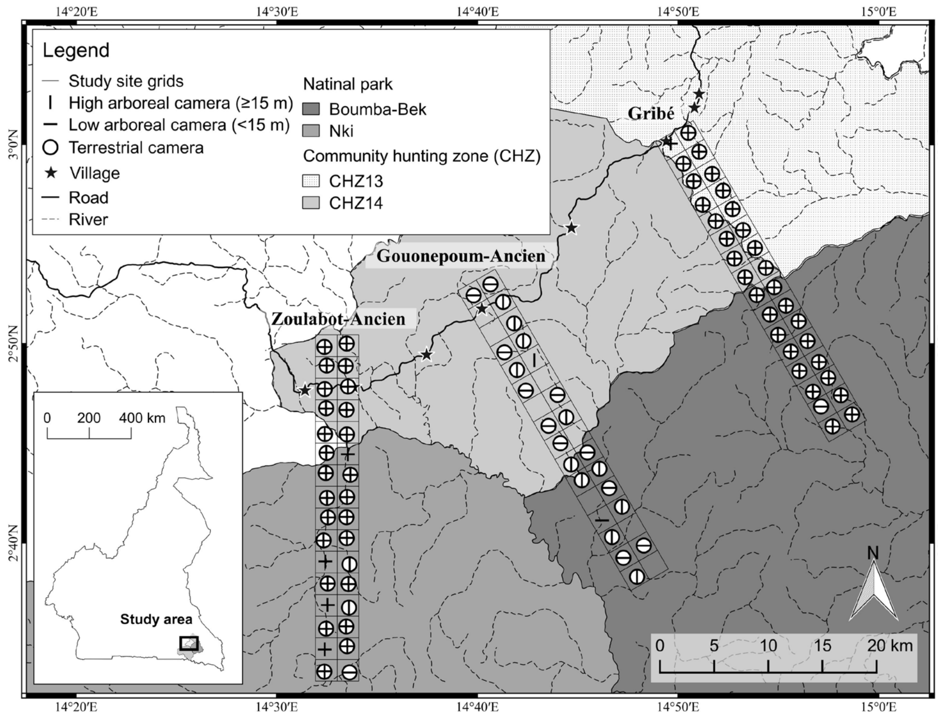


**Fig. 1.** Location of camera trap sites in rainforests in southeast Cameroon. Camera trap stations are shown only for cameras that functioned for at least one day. Overlapping symbols are a result of close placement between terrestrial and arboreal cameras (<50 m, see METHODS for details).

We established three rectangular study sites of 128 km$^2$ (4 × 32 km) extending from villages (Gribé, Gouonepoum-Ancien, and Zoulabot-Ancien) toward the national parks (Fig. 1). Cameras were deployed using a stratified random study design. Each of the three sites was divided into 32 grids of 4 km$^2$ (2 × 2 km), and we created a circle with a 250-m radius centered in each grid cell. We then generated a random point within each circle.

For terrestrial camera stations, one camera was strapped to the tree nearest to the random point in each cell at a height of 40 cm. No bait was used in this study. Terrestrial cameras were positioned parallel to the ground and facing north to avoid unwanted triggering in response the rising and setting of the sun. To maximize the probability of detecting mammals, we cleared the undergrowth in front of cameras to about 4 m.

For arboreal camera stations, we chose trees within 50 m of the terrestrial camera stations that were connected to at least one other tree by the outer branch proximities. Baka assistants then climbed the selected tree or an adjacent one, depending on which was safely accessible, and installed cameras on the trunks using metal L-brackets and wingnuts as recommended in Bowler et al. (2017).

Cameras were not baited and were set to face the target trunk or branches. The Baka assistants removed leaves and vines around cameras to avoid unwanted camera triggering by sun-warmed leaves (Gregory et al., 2014). We aimed to deploy 2 arboreal cameras in each grid, one at a height of <15 m and the other at ≥15 m (mean camera height 14.0 m ± SD 4.2 m; range, 4–24 m). However, we could not install cameras at some stations for logistical reasons. In total, we deployed cameras at 88 terrestrial and 150 arboreal stations (Gribé site: 32 terrestrial and 64 arboreal, Gouonepoum-Ancien site: 24 terrestrial and 24 arboreal, Zoulabot-Ancien site: 32 terrestrial and 62 arboreal).

## III. Data Analysis

We analyzed video footage using Timelapse version 2.2.2.5 (Greenberg & Godin, 2015; Greenberg, 2018). We identified animal species in the videos following the best available nomenclature (Kingdon et al., 2013; Kingdon, 2015). Videos were first checked by students and staff to remove empty videos that did not show any vertebrates and those showing humans, domestic dogs, and non-mammals from the data set. Staff and students identified the remaining videos containing mammals to the order level. We defined a camera trap record as the visual presence of a species in a video. Videos including only vocalizations were considered empty, and videos including two or more species were considered records for each observed species. Next, HS reviewed all mammal videos and identified mammals to the species level whenever possible. Most video observations of bats (Chiroptera), shrews (Eulipotyphla: Soricidae), rats and mice (Rodentia: Mymorpha), and squirrels and dormice (Rodentia: Sciuromorpha) were difficult to identify to the family or genus level with certainty and thus were removed from further analyses. Dwarf galagos (*Galagoides* spp., possibly including Demidoff's dwarf galagoes [*G. demidoff*] and Thomas's dwarf galagoes [*G. thomasi*]), were difficult to identify to species and were thus treated as a single taxon in subsequent analyses.

To obtain a complete list of medium- and large-sized mammals in the study area, we asked long-term researchers who had studied ecology and anthropology at this site for more than 5 years (Hattori Shiho, Hirai Masaaki, Towa Olivier William Kamgaing, and YH) for direct mammal observations. HS sent email questionnaires to these individuals on July 1, 2019. From the responses, we included direct, visual observations of living or dead animals and excluded acoustic observations, observations of mammals not identified to species level, and records from interviews with local people. We then compiled a species list for the study area using these two data sources.

To determine whether the number of species recorded from the camera traps reached an asymptote, we estimated species accumulation curves as a function of the number of terrestrial or arboreal camera stations using Kindt's exact method and employing the 'specaccum' function in the R-package 'vegan' version 2.5-5 (Oksanen et al., 2019) in R version 3.6.0 (R Core Team, 2019). Additionally, we calculated an arboreal record rate (AR) for each species using the identified camera trap records, defined as:

$$AR = (T_a / H_a) / [(T_a / H_a) + (T_t / H_t)]$$

where $T_a$ and $T_t$ are total length of videos including a given species recorded by arboreal and terrestrial cameras, respectively, and $H_a$ and $H_t$ are the sampling effort (i.e., total camera-days) of arboreal and terrestrial cameras, respectively.

We also searched for previous studies of mammal communities or hunting offtakes that had been conducted in or near our study area (Yasuoka, 2006a; 2006b; Bobo et al., 2014; Yasuoka, 2014; Bobo et al., 2015). To determine the efficiency of our survey, we compared the number of recorded species of primates (Primates), carnivores (Carnivora), and even-toed ungulates (Cetartiodactyla) between our assessment and these previous studies.

## RESULTS

Over the course of sampling, 81 terrestrial and 148 arboreal cameras functioned for at least one day; 7 terrestrial cameras experienced SD card failure, likely due to humidity, 2 arboreal cameras malfunctioned, 1 terrestrial camera was not turned on, and 1 terrestrial camera was stolen. The 229 functioning cameras recorded for a mean of 36.1 days (± 8.4 days, range: 4–56), for a total sampling effort of 2,901 and 5,404 camera-days for terrestrial and arboreal cameras, respectively. Collectively, we obtained 11,301 terrestrial and 23,643 arboreal videos. Empty videos accounted for 25.8% (2,911 videos) and 79.6% (18,807 videos) of terrestrial and arboreal videos, respectively. For 35 arboreal cameras (23.6% of the functioning arboreal cameras), empty videos accounted for >90% of total records. Cameras also detected non-mammal vertebrates such as birds, lizards, and frogs; we obtained 375 terrestrial and 1,056 arboreal bird records.

We obtained 7,359 and 4,433 camera trap records of mammals from terrestrial and arboreal cameras, respectively (Figs. 2 & 3). We identified 11,228 mammal records (95.2% of the total mammal records) to the order level and 5,455 (46.3%) to the species level, resulting in 40 species-level and 1 genus-level (*Galagoides* spp.) identifications for the study area (Table 1). Eight species and 1 genus were recorded only by arboreal cameras, and 22 species were recorded exclusively by terrestrial cameras. The remaining 10 species were captured by both camera types. The species accumulation curves of camera trap records suggested that the number of species nearly reached an asymptote for arboreal cameras, but not for terrestrial cameras (Fig. 4). Cameras recorded dwarf galagoes (*Galagoides* spp.) and 3 anomalure species, none of which had previously been observed in the study area. However, cameras did not detect 4 terrestrial mammals and 1 arboreal mammal that had been previously observed in the study area. Data representing direct observations of mammals obtained from the surveyed researchers were available for 42 species (Table 1). When these data and our camera trap observations were combined, 46 species (including a genus-level taxa *Galagoides* spp.) were considered to have been observed in the study area.

The number of recorded mammal species differed between our study and previous examples (Table 2). We recorded the largest number of primate and


**Fig. 2.** Images of mammals recorded by terrestrial camera traps in rainforests in southeast Cameroon. (a) *Gorilla gorilla*, (b) *Pan troglodytes*, (c) *Cercocebus agilis*, (d) *Atherurus africanus*, (e) *Panthera pardus*, (f) *Genetta servalina*, (g) *Xenogale naso*, (h) *Bdeogale nigripes*, (i) *Smutsia gigantea*, (j) *Potamochoerus porcus*, (k) *Tragelaphus eurycerus*, (l) *Neotragus batesi*, (m) *Philantomba monticola*, (n) *Cephalophus leucogaster*, (o) *Cephalophus nigrifrons*, (p) *Cephalophus callipygus*, (q) *Cephalophus silvicultor* and (r) *Cephalophus dorsalis*.

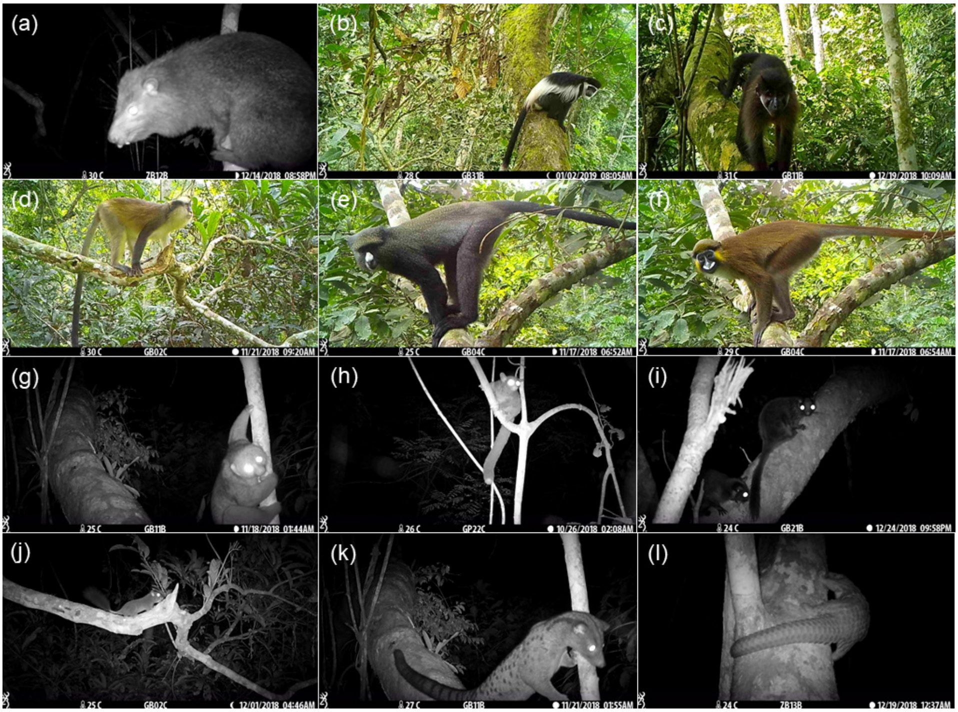


**Fig. 3.** Images of mammals recorded by arboreal camera traps in rainforests in southeast Cameroon. (a) *Dendrohyrax dorsalis*, (b) *Colobus guereza*, (c) *Lophocebus albigena*, (d) *Cercopithecus pogonias*, (e) *Cercopithecus nictitans*, (f) *Cercopithecus cephus*, (g) *Perodicticus potto*, (h) *Euoticus elegantulus*, (i) *Anomalurus derbianus*, (j) *Zenkerella insignis*, (k) *Nandinia binotata* and (l) *Phataginus tricuspis*.

carnivore species among all reviewed studies, although previous work focused on hunting that used observations and interviews (Yasuoka, 2006a; 2006b; 2014) identified more ungulate species than our study did.

## DISCUSSION

Terrestrial and arboreal camera trapping detected 40 species and 1 genus of medium- and large-sized mammals representing 89% (41 of 46 species) of the total number of species identified as present within the study area by our study or a previous publication (Table 1). Over 5 months, camera trapping detected 37 of the 42 species (88%) that had been previously observed by 4 long-term researchers. In addition, our study recorded four new taxa for the study area, all of which were small, arboreal and nocturnal.

Arboreal camera trapping was highly effective for detecting mammal species. Arboreal cameras detected all but one previously recorded species, and the species accumulation curve suggested that the number of cumulative species reached an

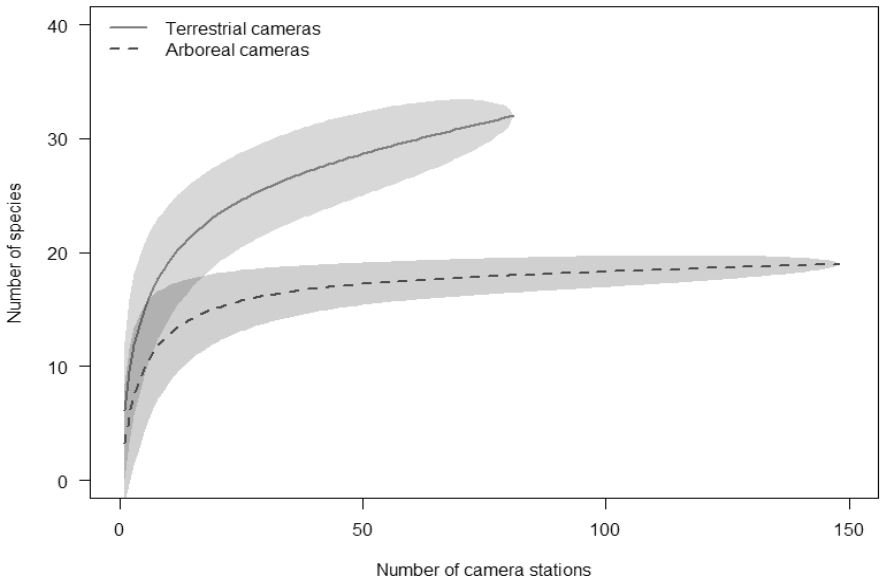


**Fig. 4.** Species accumulation curves for mammals recorded by terrestrial and arboreal camera traps in rainforests in southeast Cameroon. Lines represent the mean accumulation curves, and shaded areas represent 95% confidence intervals.

approximate asymptote at approximately 80 camera stations, on average. Moreover, the three species and one genus newly identified in the study area resulted from arboreal camera videos. Although we were not able to identify many of the small rodents observed in videos, our results suggest that arboreal camera trapping is an efficient tool for inventorying medium- and large-sized tree-dwelling mammals in African rainforests. Furthermore, we detected a much larger number of primate species, many of which are arboreal, than reported by any other study conducted in the study area (Table 2). Given that the advantages of arboreal camera traps over transect surveys were also documented for mammals in a South American rainforest (Bowler et al., 2017), we suggest that this approach may be a promising alternative to the conventional transect and recce methods for inventorying mammals in forested habitats.

Although we clearly demonstrated the advantages of arboreal camera trapping, our study also highlighted the limitations of this method. First, arboreal cameras recorded many empty videos. The proportion of empty videos was approximately three times higher in arboreal (79.6%) than in terrestrial cameras (25.8%), despite the removal of surrounding leaves and vines. These empty videos were seemingly due to the movement of leaves that had covered the field of view after deployment or that were far from the camera lens. Some arboreal cameras appeared to be placed too close to target branches (less than 1 m), and we suspect that many were empty because the animal had passed before the camera began recording.

**Table 1**. Mammal species occurring in the northern portions of Boumba-Bek and Nki National Parks and their adjacent community hunting zones (CHZs) in Cameroon. Common names follow Kingdon et al. (2013) and Kingdon (2015).

| Scientific name (Common name) | Camera-trap record: Zone (terrestrial / arboreal camera-days) | | | Camera-trap record | Direct observation record [a] |
|---|---|---|---|---|---|
| | Boumba-Bek NP (955 / 1,719) | Nki NP (635 / 1,395) | CHZs (1,311 / 2,290) | Arboreal record rate | |
| **Hyracoidea (Hyraxes)** | | | | | |
| *Dendrohyrax dorsalis* (Western tree hyrax) | ✓ | ✓ | ✓ | 1.00 | ✓ |
| **Proboscidea (Proboscids)** | | | | | |
| *Loxodonta cyclotis* (Forest elephant) | | ✓ | | 0.00 | ✓ |
| **Primates (Primates)** | | | | | |
| *Gorilla gorilla* (Western gorilla) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Pan troglodytes* (Chimpanzee) | ✓ | ✓ | ✓ | 0.05 | ✓ |
| *Colobus guereza* (Guereza colobus) | ✓ | ✓ | | 1.00 | ✓ |
| *Cercocebus agilis* (Agile mangabey) | ✓ | ✓ | ✓ | 0.02 | ✓ |
| *Lophocebus albigena* (Grey-cheeked mangabey) | ✓ | ✓ | ✓ | 1.00 | ✓ |
| *Miopithecus ogouensis* (Northern talapoin monkey) | | | | - | ✓ |
| *Cercopithecus neglectus* (De Brazza's monkey) | | ✓ | | 1.00 | ✓ |
| *Cercopithecus pogonias* (Crowned monkey) | ✓ | ✓ | ✓ | 0.98 | ✓ |
| *Cercopithecus nictitans* (Putty-nosed monkey) | ✓ | ✓ | ✓ | 0.97 | ✓ |
| *Cercopithecus cephus* (Moustached monkey) | ✓ | ✓ | ✓ | 0.82 | ✓ |
| *Perodicticus potto* (Potto) | ✓ | ✓ | ✓ | 0.99 | ✓ |
| *Euoticus elegantulus* (Southern needle-clawed galago) | ✓ | ✓ | ✓ | 1.00 | ✓ |
| *Galagoides* spp. (Dwarf galagos) [b] | ✓ | ✓ | ✓ | 1.00 | |
| **Rodentia (Rodents)** [c] | | | | | |
| *Anomalurus beecrofti* (Beecroft's anomalure) | ✓ | ✓ | ✓ | 1.00 | |
| *Anomalurus derbianus* (Lord Derby's anomalure) | ✓ | ✓ | ✓ | 1.00 | |
| *Zenkerella insignis* (Cameroon anomalure) | ✓ | ✓ | ✓ | 1.00 | |
| *Atherurus africanus* (African brush-tailed porcupine) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Thryonomys swinderianus* (Greater cane rat) | | | ✓ | 0.00 | ✓ |

| | | | | | |
|---|---|---|---|---|---|
| **Carnivora (Carnivores)** | | | | | |
| *Mellivora capensis* (Ratel) | | | | - | ✓ |
| *Nandinia binotata* (African palm civet) | ✓ | ✓ | ✓ | 0.23 | ✓ |
| *Panthera pardus* (Leopard) | | ✓ | | 0.00 | ✓ |
| *Profelis aurata* (African golden cat) | | ✓ | | 0.00 | ✓ |
| *Genetta servalina* (Servaline genet) | ✓ | ✓ | ✓ | 0.01 | ✓ |
| *Poiana richardsoni* (Central African oyan) | ✓ | ✓ | ✓ | 0.37 | ✓ |
| *Civettictis civetta* (African civet) | | | | - | ✓ |
| *Xenogale naso* (Long-nosed mongoose) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Atilax paludinosus* (Marsh mongoose) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Bdeogale nigripes* (Black-legged mongoose) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Crossarchus platycephalus* (Cameroon cusimanse) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| **Pholidota (Pangolins)** | | | | | |
| *Phataginus tricuspis* (Tree pangolin) | ✓ | ✓ | ✓ | 0.08 | ✓ |
| *Smutsia gigantea* (Giant pangolin) | ✓ | | | 0.00 | ✓ |
| **Cetartiodactyla (Even-toed ungulates)** | | | | | |
| *Potamochoerus porcus* (Red river hog) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Hylochoerus meinertzhageni* (Forest hog) | | | | - | ✓ |
| *Hyemoschus aquaticus* (Water chevrotain) | | ✓ | ✓ | 0.00 | ✓ |
| *Syncerus caffer* (African buffalo) | | | | - | ✓ |
| *Tragelaphus spekii* (Sitatunga) | | | ✓ | 0.00 | ✓ |
| *Tragelaphus eurycerus* (Bongo) | ✓ | | | 0.00 | ✓ |
| *Neotragus batesi* (Bates's pygmy antelope) | ✓ | | ✓ | 0.00 | ✓ |
| *Philantomba monticola* (Blue duiker) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Cephalophus leucogaster* (White-bellied duiker) | ✓ | ✓ | | 0.00 | ✓ |
| *Cephalophus nigrifrons* (Black-fronted duiker) | ✓ | ✓ | | 0.00 | ✓ |
| *Cephalophus callipygus* (Peters's duiker) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Cephalophus silvicultor* (Yellow-backed duiker) | ✓ | ✓ | ✓ | 0.00 | ✓ |
| *Cephalophus dorsalis* (Bay duiker) | ✓ | ✓ | ✓ | 0.00 | ✓ |

[a] Records of direct observations by 4 long-term researchers, see text for details.
[b] Camera-trap videos of *Galagoides* spp., possibly including *G. demidoff* and *G. thomasi*.
[c] Mymorpha (rats and mice) and Sciuromorpha (squirrels and dormice) were excluded from species-level identification.

**Table 2.** Methodology and number of mammal species recorded by the present study, along with previous examples from the study area.

| Method | Study period (month) | Sampling effort | Number of recorded species | | | References |
|---|---|---|---|---|---|---|
| | | | Primates | Carnivora | Cetartiodactyla | |
| Camera-trapping | 5 | 8,305 camera-days | 12 | 9 | 11 | This study |
| Direct observation (including carcasses) | 2 | 398-km walk on transects and trails | 4 | 0 | 4 | Bobo et al. (2014) |
| Direct observation of hunted animals | 2 | Hunter follow for 899 hunter-days | 8 | 6 | 9 | Bobo et al. (2015) |
| Direct observation and interview | 7 | Visits to 7 snare hunting sites | 5 | 5 | 12 | Yasuoka (2006a; 2006b; 2014) |

Empty videos are problematic because they fill memory cards, drain batteries, and require extensive time to review. Determining the suitable distance between the target and the camera (Suzuki & Ando, 2019) and regularly monitoring the vegetation surrounding cameras may improve survey efficacy.

Secondly, previous studies in Peruvian rainforests (Gregory et al., 2014; Bowler et al., 2017) reported that arboreal camera trapping required specialized climbing techniques and considerable time (2–10 h per camera station). In this regard, we were able to effectively and safely deploy cameras thanks to the Baka assistants, who use sophisticated climbing techniques in their daily lives (Kraft et al., 2014). In our example, placing 2 arboreal cameras within a grid required only 30–180 min, although we note this was longer than the time required to install a terrestrial camera (10–20 min). Therefore, cooperation and partnership with local people may be crucial for effective arboreal camera trapping.

We configured cameras to record short videos instead of still photos to increase the likelihood of distinguishing among morphologically similar species. For example, we were able to identify four species of "red duikers" (*Cephalophus leucogaster*, *C. nigrifrons*, *C. callipygus*, and *C. dorsalis*) when individuals were <3 m from the camera (Fig. 2n, o, p, and r). Video images allowed us to confirm species-specific features including face length, dorsal line pattern, and buttock color. Videos were also advantageous when distinguishing among the 3 anomalure species and among small carnivore species. We strongly recommend the use of video in mammal inventories, despite its effect on battery life and the increased time required for image sorting relative to photos.

Our results highlighted important considerations for camera placement. Despite a large sampling effort, we did not record 5 mammal species known from the study area (Table 1). Two of these, the ratel *Mellivora capensis* and the forest hog *Hylochoerus meinertzhageni*, are considered very rare (Nzooh Dongmo et al., 2016). To record rare species, it may be beneficial to rotate cameras to new sites after a given period of time, rather than maximizing time in one area (Si et al., 2014). The remaining three undetected mammals have specific habitat preferences. African civets (*Civettictis civetta*) prefer degraded forests (Ray, 2013), African buffaloes (*Syncerus caffer*) depend on grassy glades and watercourses (Prins &

Sinclair, 2013), and northern talapoin monkeys (*Miopithecus ogouensis*) are specialized to riverine and swamp forests (Groves & Kingdon, 2013). We utilized a stratified-random design and did not place cameras on game trails or within specific environments to avoid biasing the sampling toward specific species (Rowcliffe & Carbone, 2008). However, we note that additional, targeted cameras placed in specific habitats may be necessary to ensure video capture of all mammals within an area.

We demonstrated that the concurrent use of arboreal and terrestrial camera traps is a powerful tool for inventorying medium- and large-sized mammals. Arboreal cameras effectively recorded most of the tree-dwelling species in the study area and provided new species records. Careful camera placement and the use of video rather than photos will enhance the efficacy of future camera trap surveys. We acknowledge that, as with all survey techniques, multi-layer camera trapping has disadvantages. We were unable to identify volant and small species to the family or genus level, and our design precluded capture of aquatic and subterranean species. However, the combined use of arboreal and terrestrial traps showed significant advantages over conventional field methods for mammal inventory in African rainforests. Field scientists and practitioners who aim to gather complete species richness data within forested sites are encouraged to consider multi-layer camera trapping in future surveys.

ETHICS STATEMENT This study complied with the laws of the Republic of Cameroon and was conducted with approval from the Ministry of Scientific Research and Innovation (MINRESI, N°0190/ MINRESI/Projet COMECA/PM/07/2018). Access to Boumba-Bek and Nki National Parks was approved by the Ministry of Forestry and Wildlife (MINFOF, N°1527/L/MINFOF/SETAT/SG/DFAP/SDCF/SEP/EP).

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Correspondig Author's Name and Address: HONGO Shun, *The Centre for African Area Studies, Kyoto University, 46 Yoshida Shimoadachi-cho, Sakyo-ku, Kyoto 606-8501, JAPAN.*

E-mail: hongo.shun.8s [at] kyoto-u.ac.jp